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MORPHOLOGICAL STUDIES OF ARCHEOLOGICAL AND RECENT COCA LEAVES (*ERYTHROXYLUM* SPP.)

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INTRODUCTION

Coca leaves, derived from two closely related species of the genus *Erythroxylum* P. Br., are widely used in South America as a masticatory and in household medicine. The history of coca chewing dates back several thousand years and there is evidence that coca is one of the oldest domesticated plants in the New World (Plowman, in press). Coca continues to be an important cultural feature among indigenous peoples throughout the Andes and in the western Amazon. In recent years, the cultivation of coca has greatly increased in order to supply the great demand for the alkaloid cocaine, which has become an extremely popular recreational drug in Western societies.

In spite of its great antiquity, the history and botany of coca have not been studied in depth until the past decade. Although

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coca was formerly considered to be derived from the single species *Erythroxylum Coca* Lam., modern studies have demonstrated that two distinct species are involved: *E. Coca* Lam. and *E. novogranatense* (Morris) Hieron. In addition, each of the two species has a distinct variety, so that four cultivated cocas are now recognized: *E. Coca* Lam. var. *Coca, E. Coca* var. *Ipadu* Plowman, *E. novogranatense* (Morris) Hieron. var. *novogranatense* and *E. novogranatense* var. *truxillense* (Rusby) Plowman (Plowman 1979a, b, 1981, 1982; Rury, 1981, 1982; Bohm, Ganders & Plowman, 1982; Plowman & Rivier, 1983; Plowman, in press). The present distribution of the four varieties is shown in Plate 32.

All four of the cultivated cocas were domesticated in pre-Columbian times and are still employed by native coca chewers in South America. Each was known by a different name before the Spanish popularized the now widespread term "coca". All of the cultivated cocas contain cocaine, although they are now known to differ appreciably in their content of minor alkaloids and other chemical constituents (Bohm, Ganders & Plowman, 1982; Plowman & Rivier, 1983). Additional important differences among the four varieties, which hitherto had been overlooked, are found in their leaf and stem anatomy, ecology, geographical distribution, breeding relationships, as well as in their cultivation and preparation for chewing. These differences have arisen through intensive human selection over a long period of time for desirable traits and for adaptations which permit coca cultivation in a wide variety of habitats.

Erythroxylum Coca var. *Coca,* "Huánuco" or "Bolivian" coca, is thought to be the most nearly ancestral type and today is still found in a wild or feral state throughout the moist tropical forests ("*montaña*") of the eastern Andes of Peru and Bolivia. It is also extensively cultivated today as the most important commercial source of coca leaves and cocaine.

Amazonian coca, *E. Coca* var. *Ipadu,* is cultivated in the lowland Amazon by a number of tribes of shifting agriculturalists. It apparently has been derived relatively recently as a lowland cultigen from *E. Coca* var. *Coca* of the Andean foothills, and does not persist as a feral plant in the forests of

Amazonia. Amazonian coca leaves are always finely pulverized before use in contrast to other varieties in which the whole leaf is chewed (Plowman, 1981; Schultes, 1981).

Trujillo coca is classified as *E. novogranatense* var. *truxillense,* based upon its morphology, ecology and alkaloid and flavonoid chemistry. It is, however, intermediate in a number of characteristics between *E. Coca* var. *Coca* and *E. novogranatense* var. *novogranatense* and may represent a stage in a linear evolutionary sequence between these two taxa (Bohm, Ganders & Plowman, 1982). Trujillo coca is well adapted to dry areas and shows remarkable resistance to drought. Today it is grown only in the river valleys of north coastal Peru and in the arid valley of the upper Río Marañón, with one disjunct population in northwestern Ecuador (Plowman, 1979b). It is not found anywhere in a wild or feral state and must be considered a true cultigen. Trujillo coca probably evolved under domestication from *E. Coca* var. *Coca* in the drier valleys of northern Peru or southern Ecuador and only later diffused to coastal Peru.

Colombian coca, *E. novogranatense* var. *novogranatense,* is cultivated in both wet and dry areas in the mountains of Colombia but, like Trujillo coca, exhibits tolerance to drought. It is also identical to Trujillo coca in its alkaloid and flavonoid chemistry (Bohm, Ganders & Plowman, 1982; Plowman & Rivier, 1983). Unlike the other cultivated varieties, Colombian coca is partially self-compatible and appears to be the evolutionarily most derived species.

Dating of the time of divergence of the species and varieties of cultivated coca has not yet been possible. Application of techniques of biochemical genetic markers may prove useful toward this end but have not yet been investigated in *Erythroxylum.* A second approach, which has been useful in unraveling the early evolutionary history of many domesticated plants, is the study of dated archeological remains.

ARCHEOLOGICAL COCA

The early evolution of coca in light of archeological evidence recently has been reviewed in detail by Plowman (in press). The first evidence for coca chewing appears in the Valdivia culture on the Santa Elena Peninsula in southwestern Ecuador in the form of small, ceramic lime containers, dating about 2000 B.C. A small figurine representing a coca chewer was also found here and dates to Late Valdivia (1500–1600 B.C.) (Lathrap et al., 1976). More recent artifacts from Ecuador, Colombia and Peru demonstrate a long and continuous tradition of coca chewing (Bray & Dollery, 1983; Plowman, in press).

Archeological specimens of actual coca leaves are extremely scarce, often poorly preserved, and usually lack stratigraphic or carbon-14 dates. In many cases, leaves reputed to be coca from archeological sites have not been preserved by archeologists for later examination and verification by specialists. As a result, many critical specimens are now completely lost or discarded.

Most specimens of archeological coca originate from the dry Peruvian coast, where preservation of plant remains is optimal. The first suggestion of archeological coca dates to the end of the Late Preceramic Period 6 (1800–2500 B.C.). Engel (1963) found leaves "looking like coca" along with large deposits of burnt lime (presumably used as an alkaline catalyst in coca-chewing) at the site of Asia in the Omas Valley in central Peru. Asia is radiocarbon-dated at about 1300 B.C. but probably dates to about 1800 B.C. (M. Moseley, pers. comm.). Engel's report of coca at this early site must be considered dubious since the specimens no longer exist. Patterson (1971) excavated preserved coca leaves at Las Gaviotas near Ancón, a site dated between 1750 and 1900 B.C.; Cohen (1978) also reported coca from Ancón with a date of 1400–1800 B.C. Coca leaves were also one of the items (along with maize and marine shells) stockpiled in a group of storage structures at Huancayo Alto in the Chillón Valley, dating between 200–800 B.C. (Dillehay, 1979). None of these earliest records of archeological coca have been botanically identified.

Preserved coca leaves from much later sites on the Peruvian coast have been available for study and form the basis of the present investigation (Table 1). These include specimens from Vista Alegre in the Rimac Valley (ca. 600–1000 A.D.), which were illustrated by Towle (1961, Plate IV: 5); from the Yauca Valley (Late Horizon, Plates 35 and 36); from Monte Grande in the Río Grande Valley and in the environs of Nazca ("Cultura Nazca"); from the Taruga Valley (Plates 33 and 34) and Ocucaje (Late Horizon) and at Chacota near Arica in northermost Chile (Inca Period).

Griffiths (1930) has made the only detailed anatomical study of archeological coca leaves from a grave at Nazca. Based on comparison with commercial coca leaves, she concluded that they belonged to the variety then known as "Peruvian" coca, an earlier pharmaceutical trade name for Trujillo coca. Our re-examination of her data and illustrations confirm the identity of her specimens as Trujillo coca, although we have not located her original material. Griffith's leaf illustrations conform entirely to our typological concept of Trujillo coca in both qualitative and statistical aspects of foliar size, form, venation and anatomy.

Towle (1952) reported "leaf tissue found rolled into a quid" in a mummy bundle from the Paracas Necropolis on the southern coast of Peru and noted that it "would suggest the leaves of coca (*Erythroxylum Coca* Lam.)." Towle was apparently unfamiliar with Griffith's earlier study and did not have authentic material of Trujillo coca for comparison. She concluded that the leaf fragments were "too small and brittle" to permit their botanical identification.

Coca endocarps from Nazca were identified by Griffiths (loc. cit.) as Trujillo coca, whereas those found at Vista Alegre were referred to "*Erythroxylum Coca*" by Towle (1961). More recently, endocarps were excavated at Chilca (Late Intermediate Period) by Jeffrey Parsons (pers. comm.). Although not included in the present study, all archeological coca endocarps which we have examined are referable to Trujillo coca.

In the present contribution, we examine the leaf morphology and anatomy of available archeological leaf specimens and compare them with modern samples of leaves of the cultivated cocas presently grown in South America. Because archeological material often provides only isolated or fragmented leaves, as noted by Towle (1952), it is essential to consider in detail the microscopic features of coca leaves of each variety and compare them with the same characters in the archeological specimens.

As an aid to the identification of coca leaves and leaf fragments, we have summarized in Table 3 those structural details which are useful in the determination of cultivated coca leaf specimens. Details of foliar venation are presented in Table 4 and selected leaf anatomical features are presented in Table 5. A comprehensive review of taxonomically useful leaf structural features in *Erythroxylum* can be found in an earlier publication (Rury, 1981).

MATERIALS

Archeological coca specimens were obtained from the following museum collections: Ethnobotany Laboratory, Botanical Museum, Harvard University; Lowie Museum of Anthropology, University of California, Berkeley; and the Museo de Historia Natural 'Javier Prado', Lima, Peru. Additional specimens of archeological leaves were studied at the Peabody Museum of Archaeology and Ethnology, Harvard University, and of coca endocarps from the collection of Dr. Jeffrey Parsons. All of these specimens originated in coastal Peru or adjacent northernmost Chile; in most cases the leaves were included in woven coca bags found in burials. The specimens at the Museo de Historia Natural 'Javier Prado' were originally found in coca bags preserved at the Museo Regional de Ica, Peru. They were supplied by the director, Sr. Alejandro Pezzia A. to Dra. Maria Rostworowski, who in turn presented them to Dr. Ramón Ferreyra for identification (cf. Rostworowski, 1973: 205). The archeological coca specimens are listed in Table 1.

Recent specimens of cultivated coca varieties were taken from the herbarium specimens listed in Table 2. Location of voucher specimens (including duplicate specimens) are listed according to herbarium abbreviations suggested by Holmgren, Keuken and Schofield (1981). All recent coca specimens were determined by Plowman.

METHODS

Six archeological (Table 1) and thirty recent (Table 2) leaf specimens of the cultivated cocas were prepared for microscopic examination. All of these leaves were cleared in a 5% aqueous solution of NaOH, either at room temperature (archeological), or in an oven at ca. 70° C. (recent). Cleared leaves were stained with a 1% solution of safranin in 50% ethanol for several days, then dehydrated with ethanol, treated with xylene and mounted permanently on microscope slides in Canada balsam. Recent leaves also were prepared for paraffin sectioning by conventional methods of botanical microtechnique. To obtain epidermal sheets for stomatal examination and counts, leaf fragments were macerated in Jeffrey's macerating solution recipe from Johansen (1940).

Numbers of freely terminating veinlets and stomata per mm^2 of leaf surface were microscopically determined, using 10–20 counts per leaf or leaf fragment. Stomatal counts and maximum guard cell lengths were measured either from cleared leaves (archeological) and/or macerated leaf epidermal sheets (recent). In order to provide a reliable comparison of their stomatal systems, the stomatal density (i.e. number per mm^2) was corrected for relativistic differences in guard cell length among different specimens. Since stomatal size and relative number per unit of leaf area typically are inversely interrelated (Rury, 1981, 1982), it was necessary to calculate the percentage of leaf surface occupied by stomata (i.e. stomatal frequency) for comparative purposes. This calculation thus integrates guard cell length and stomatal density into a single, standardized measurement, which is especially useful when working with leaf fragments.

Leaf venation terminology has been simplified as much as possible, but follows that of Mouton (1970) and Hickey (1973) with necessary additions and modifications.

Illustrations were prepared using several techniques. Negative prints of foliar venation patterns of recent coca leaves were prepared by placing cleared leaf slides directly in the photographic enlarger (Dilcher, 1974). Line drawings of foliar venation and epidermal patterns were made for all specimens, using a Wild dissecting microscope with a drawing attachment. Several black and white photomicrographs of high order leaf venation, in both archeological and recent specimens, were made with a Zeiss photomicroscope, either with or without polarizing filters.

RESULTS

Archeological Leaf Specimens (*Erythroxylum novogranatense* var. *truxillense*)

LEAF FORM: Leaves are relatively small in size, ranging from 23–40 mm. in length and 6–16 mm. in width. The leaf blade shape is mostly lanceolate, narrowly elliptic, or slightly oblanceolate. Leaf bases are typically cuneate, with acute and conspicuously mucronulate apices. The central panel, demarcated by abaxial (on lower surface), longitudinal lines along either side of the midvein, is usually faint or sometimes absent, but may be prominent and enclose a finer reticulum of less conspicuous venation when compared with the exmedial (outer) portions of the leaf blade.

LEAF VENATION: The primary vein (midvein) is moderately thick and follows a straight course from the leaf base to the apex. The basic vein pattern is only slightly variable, ranging between the eucamptodromous and brochidodromous configurations, with a festooned system of higher order, intramarginal, loop-forming veins (Plate 37).

The basic vein patterns derive their appearance from the course and behavior of the secondary veins, in relation to one another, the midvein and the leaf margin. Each leaf contains from 7–15 slender, secondary veins which typically diverge from the midvein at moderately to widely acute angles (45–80°) and follow a sinuous or smoothly upcurving course as they approach the leaf margin. These secondary veins then either (1) taper into a system of festooned, high order, intramarginal loops along the outer flanks of the superadjacent secondary veins (eucamptodromous) or (2) recurve towards the midvein and join the outer flanks of the superadjacent secondary veins to form a series of secondary vein arches (brochidodromous). The intercostal areas demarcated by these secondary veins are moderately uniform in their size and shape. Intersecondary veins of composite origin from the coalescence of tertiary veins, although few in number (2–7 per leaf), may occur within the intercostal areas. Intramarginal veins of secondary origin are absent from all leaves examined.

Slender tertiary veins arise at widely acute to slightly obtuse angles (80–110°) along the inner and outer flanks of the secondary veins. These tertiary veins ramify towards the midvein and/or transversely within the intercostal areas to form a ramified, random reticulum of non-oriented, polygonal, tertiary areoles. These tertiary areoles are further subdivided by ramified fourth and fifth order veinlets into a random reticulum of many, moderately well developed and small, polygonal or quadrangular areoles. The mean number of freely terminating veinlets ranges between 16–30 per mm^2, with an overall mean of 22 per mm^2 (Table 4). Veinlet terminations are typically tracheoid with spiral or pitted secondary cell walls (Plate 38). Tracheoidal idioblasts and fibrous sclereids were absent from all leaf specimens examined. The marginal ultimate venation of these leaves consists of second through fourth order, loop-forming veins and veinlets, which promote the "festooned" appearance of the overall venation patterns.

EPIDERMIS: The epidermal cells of all leaves are polygonal in surface view, with straight walls. Cells of the upper epidermis are of uniform size but are consistently larger than those of the lower epidermis. Cells of the lower epidermis, however, may reveal a greater degree of size variation than those of the upper epidermis.

In all leaves, stomata are restricted to the lower surface and are strictly of the paracytic type, with one pair of subsidiary cells aligned parallel to the long axis of each stomate (Plate 37E, F). Guard cell lengths do not exceed 25μm in any of the stomata, and mean stomatal density ranges between 156–203 per mm^2, with an overall mean of 183 per mm^2 (Table 5). Stomatal frequency, calculated as the relative percentage of leaf surface occupied by stomata, averages 11.4%, and specimen means range between 10–13% (Table 5).

Epidermal papillae are either absent (e.g. Nazca #8), sparse or prominent, but are consistently restricted to the lower epidermal cells (Plate 37D, E, F). Papillae are always absent from both the guard cells and their associated subsidiary cells of all stomata on the lower leaf surface.

CRYSTALS: Vein-associated prismatic or rhomboidal crystals of calcium oxalate are typically very abundant and may occur also in cells of either epidermal surface (Plate 38).

FOLIAR SCLEREIDS: No foliar sclereids of any type were observed in the archeological leaves examined.

Recent Leaf Specimens

LEAF FORM AND VENATION: Although leaves of the cultivated cocas may exhibit similar and intergrading forms and patterns of low and high order venation, a typological concept of leaf form and venation can be formulated for them. The leaf venation patterns which are considered "typical" for each of the cultivated cocas are summarized in Table 4. These diagnoses are based on observations of many more specimens than were prepared for microscopic study (Table 2), and microscopic examination was performed only on selected specimens which represent the full range of variability within each variety. Leaves of Amazonian coca (*Erythroxylum Coca* var. *Ipadu*) are not sufficiently distinct from those of *E. Coca* var. *Coca* in their leaf venation to warrant separate description. It should be noted, nevertheless, that particular leaf specimens may diverge from this overall diagnosis in details of both low and high order venation as well as in leaf form.

Leaves are small to medium in size, ranging from 20–115 mm. in length and 10–24 mm. in width. Leaves of Trujillo coca typically are the smallest, whereas those of Amazonian coca attain the largest sizes. All varieties of cultivated coca possess an acute or cuneate leaf base. Leaf shape varies both within and among varieties, but may be characterized as follows for each variety: (1) *E. Coca* var. *Coca*, broadly lanceolate to elliptic, with an acute and conspicuously mucronulate apex; (2) *E. Coca* var. *Ipadu,* broadly elliptic, with an acute to obtuse, conspicuously mucronulate apex; (3) *E. novogranatense* var. *novogranatense,* oblong to oblong-elliptic (rarely obovate), with an obtuse to rounded or emarginate, rarely mucronulate apex; and (4) *E. novogranatense* var. *truxillense,* narrowly elliptic to lanceolate, with an acute, minutely mucronulate apex. Although foliar form is more or less diagnostic for particular coca varieties, the full range of variation among the leaves of the four varieties constitutes a continuum of shapes and sizes (Plate 39). Isolated leaves and leaf fragments, therefore, cannot be reliably identified on the basis of leaf form and size alone. A combination of both macro- and micromorphological features is required for accurate taxonomic identifications of coca leaves.

The central panel, demarcated by a pair of abaxial "lines" (anatomically, collenchyma ridges; Rury, 1981) running parallel to and on either side of the midvein, is of variable occurrence and prominence among the cultivated cocas. The central panel may be conspicuous, due to its markedly finer and less prominent vein reticulum in *E. Coca* var. *Coca* and *E. novogranatense* var. *novogranatense,* but often is very faint or entirely lacking in some leaves of *E. Coca* var. *Ipadu* and *E. novogranatense* var. *truxillense,* owing to overall uniformity of the vein reticulum throughout the leaf. Statistically significant differences may occur in both stomatal and veinlet termination numbers, within versus outside of the central panel, when this feature is prominent in leaves of each variety (Rury, 1982). Careful attention, therefore, must be given to the position in the leaf at which such data are gathered.

The primary vein (midvein) is of moderate diameter and follows a straight course from the leaf base into its apex. The basic venation patterns vary moderately, both within and among coca varieties, ranging from eucamptodromous to brochidodromous, with a festooned system of intramarginal, loop-forming veins and veinlets (Table 4). Leaves of *E. novogranatense* var. *truxillense* (Trujillo coca) are the most variable of all varieties in their overall venation pattern, which may range between the eucamptodromous type characteristic of both varieties of *E. Coca* and the brochidodromous pattern typical of *E. novogranatense* var. *novogranatense.* As will be discussed in greater detail later, such extensive variation in leaf form and venation can usually be explained ecologically, in relation to differences in microhabitat experienced by individual leaves or plants, but it is also an indication of the intermediate nature of Trujillo coca between *E. Coca* var. *Coca* and *E. novogranatense* var. *novogranatense.*

Secondary veins of both varieties of *E. Coca* typically are numerous (15–40 per leaf), closely spaced and of moderate thickness. In both varieties of *E. novogranatense,* they are usually fewer (8–18 per leaf), more widely spaced and more slender (Plate 39). Secondary vein divergence angles from the midvein range between widely acute to perpendicular (80–90°, *E. Coca* vars., *E. novogranatense* var. *truxillense*) and narrowly to widely acute (40–80°, *E. novogranatense* var. *novogranatense,* some specimens of *E. novogranatense* var. *truxillense*). Secondary veins follow an initially straight, regular (*E. Coca* vars.) or sinuous (*E. novogranatense* vars.) course, and gradually upcurve as they approach the leaf margins. The subsequent branching behavior of these veins determines the basic configuration of the overall venation pattern. These secondary veins then either: (1) taper into a festooned system of high order, intramarginal loops along the outer flanks of the superadjacent secondary veins (eucamptodromous, *E. Coca* vars.) or (2) recurve admedially (inward towards midvein) near the margin and join these superadjacent secondaries at widely acute to obtuse angles (80–100°) to form a series of (secondary) vein arches (brochidodromous, *E. novogranatense* var. *novogranatense*). Secondary veins of *E. Coca* varieties and *E. novogranatense* var. *truxillense* normally are thicker, more prominent and more numerous than in leaves of *E. novogranatense* var. *novogranatense.* Secondary veins thus demarcate intercostal areas which are both more numerous and of greater uniformity in size and shape in leaves of *E. Coca* varieties and *E. novogranatense* var. *truxillense* than in most leaves of *E. novogranatense* var. *novogranatense.* Intersecondary veins of composite origin are very few, but when present they are most numerous in the larger intercostal areas of *E. novogranatense* var. *novogranatense*. Intramarginal veins of secondary origin are absent from leaves of all varieties.

Slender tertiary veins arise at widely acute to slightly obtuse angles (80–100°) along the admedial (inner) and exmedial (outer) flanks of the secondary veins and ramify within the intercostal areas to form non-oriented, polygonal, tertiary areoles of various sizes. Tertiary areoles tend to be slightly smaller and most numerous in both varieties of *E. Coca*. Conversely, leaves of *E. novogranatense* var. *novogranatense* typically have fewer but larger intercostal areas and tertiary areoles than do those of either variety of *E. Coca*. Leaves of *E. novogranatense* var. *truxillense* are often intermediate in this respect but may reveal the full range of patterns exhibited collectively among leaves of the other three varieties (Plate 40).

All tertiary areoles are subdivided by a random reticulum of slender, fourth and fifth order veinlets, which constitute a moderately well developed system of small, non-oriented, polygonal and quadrangular areoles. This system of areoles is best developed (i.e. most completely closed) and contains more numerous areoles in both varieties of *E. Coca*, whereas leaves of *E. novogranatense* varieties normally have a more open system of fewer and slightly larger areoles (Plates 39 and 40).

The relative number of freely terminating veinlets in coca leaves serves as a quantification of qualitative differences in high order venation and areolation among the four cultivated varieties. Leaves of *E. Coca* varieties often contain fewer veinlet termini per mm^2 and thus have more numerous ultimate areoles than do those of either variety of *E. novogranatense* (Table 5; Plates 39 and 40). Although leaves of *E. novogranatense* var. *truxillense* have the highest veinlet termination numbers of all coca varieties, they may show a degree of variation equal to that observed collectively among the other three varieties, as is the case with qualitative aspects of their form and venation (Table 5). Veinlet termini are typically tracheoid with spiral or pitted secondary walls (Plate 40). Tracheoid idioblasts were not observed in any variety.

The marginal ultimate venation of all coca leaves consists of second through fourth order, loop-forming veins which promote its "festooned" appearance due to the nearly complete closure of the intramarginal, loop-forming veinlets.

EPIDERMIS: Epidermal cells typically are polygonal in surface view with straight lateral walls. The cells are larger in the upper epidermis, although their sizes are normally uniform within each surface layer. Epidermal cell walls appear slightly sinuous only rarely in occasional specimens of *E. novogranatense* var. *novogranatense*.

Stomata are of the paracytic type, with their paired subsidiary cells aligned parallel to the long axis of the guard cells, and are restricted to the lower epidermis in all leaves (Plate 37). Statistical data for stomatal density, frequency and guard cell size are summarized in Table 5.

Epidermal papillae are prominent and abundant but confined to the lower surface of the leaves. They are always absent from the guard cells and associated subsidiary cells of the stomatal apparatus.

CRYSTALS: Vein-associated, prismatic (rhomboidal) crystals of calcium oxalate may be abundant, sparse or absent in all coca leaf varieties. Prismatic crystals also may occur in clusters of anticlinally subdivided cells of the lower and upper epidermis in all varieties.

FOLIAR SCLEREIDS: Foliar sclereids are typically absent from all cultivated coca leaves but may be characteristic of other species of *Erythroxylum* (Rury, 1981, 1982).

DISCUSSION

LEAF STRUCTURAL PLASTICITY OF COCA LEAVES

Light intensity, humidity and moisture availability may influence profoundly the relative leaf size, form, vein thickness and patterns, as well as stomatal and veinlet terminus numbers in all varieties of cultivated coca (Rury, 1981, 1982). Classical shade-leaf as opposed to sun-leaf structural differences may be found within each variety in relation to microhabitat differences experienced by individual plants and leaves. Humid and shady microhabitat conditions result normally in the development of relatively large, thin leaves with reduced numbers of stomata and veinlet termini per unit area, as well as more slender and less conspicuous veins. Conversely, sunny and drier habitats induce the formation of small and thicker leaves with comparatively more numerous stomata and veinlet termini, and more prominent, thicker veins. Shade-leaf morphology appears not only in South American coca plants grown under shaded conditions, but also in plants of each variety cultivated under glass at temperate latitudes in North America (Rury, 1982; Plate 39D, E). Due to this habitat-related plasticity in the structure of coca leaves as well as their intergrading patterns of leaf structural variation among the four varieties, identifications of coca leaves and leaf fragments are often problematic (and ill-advised) in the absence of relevant ecological and geographic data for the specimens under consideration. The taxonomically most useful structural features of cultivated coca leaves are summarized in Table 3.

COMPARISON OF ARCHEOLOGICAL AND RECENT COCA LEAVES

Although superficially similar in form and venation, leaves of the four modern varieties of cultivated coca can be distinguished on the basis of subtle differences in shape and size, central panel prominence, details of low and high order venation, and stomatal features, especially when such data are integrated with ecological and geographic information for the specimens. On similar grounds, it is possible to determine the specific and varietal affinities of archeological coca leaves.

Selected leaf structural features of both archeological and recent coca plants from South America are summarized in Table 5. These statistical data are of taxonomic value, however, only when assessed together with qualitative aspects of leaf structure. The archeological leaves studied here clearly are more similar to recent leaves of the cultivated cocas than to any wild species of *Erythroxylum* (see Tables 3, 4). Although several wild species of *Erythroxylum* of the neotropical section *Archerythroxylum* (*sensu* Schulz, 1907) may resemble cultivated coca varieties in their leaf structure, the archeological leaves studied here are easily distinguished from any wild "coca mimics" (Rury, 1981, 1982).

Features shared by archeological and recent coca leaves include their: (1) size and form; (2) variable prominence of a central panel on the lower leaf surface; (3) patterns of low and high order venation; (4) comparable numbers of freely terminating veinlets per mm^2 of leaf area; (5) polygonal epidermal cells with straight (anticlinal) walls; (6) epidermal papillae restricted to the lower leaf surface; (7) paracytic stomata of similar dimensions and numbers, also restricted to the lower leaf surface; and (8) numerous prismatic crystals associated with veins and occurring within subdivided epidermal cells.

All archeological coca leaves studied here are morphologically identical to recent leaves of Trujillo coca (*E. novogranatense* var. *truxillense*) in their small size, mostly lanceolate shape, acute leaf apices and cuneate leaf bases, as well as their reduced prominence of a central panel. As in recent Trujillo coca, the archeological leaves reveal a basic foliar venation pattern which is intermediate between the characteristic eucamptodromous configuration of *E. Coca* var. *Coca* and the slender-veined, brochidodromous pattern of most leaves of *E. novogranatense* var. *novogranatense*. Details of leaf venation in the archeological leaves which conform to our typology for Trujillo coca include: (1) the divergence angles and irregular course of the secondary veins; (2) an intermediate number of secondary veins and intercostal areas; (3) a relatively incomplete (open) system of high order venation, with (4) a rather large number of freely terminating veinlets.

Statistical details of *Erythroxylum* leaf structure are both ecologically more variable and taxonomically less reliable than qualitative aspects of foliar form, venation and anatomy. Nevertheless, our archeological leaves fall clearly within the range of statistical variation in stomatal and venation systems observed among leaves of all four modern coca varieties (Table 5). The archeological leaves are more similar in these features to both varieties of *E. novogranatense* than to either variety of *E. Coca*, but most closely resemble leaves of Trujillo coca in their larger stomata, reduced stomatal frequency and higher number of veinlet termini (Table 5).

Surprisingly, the archeological leaves examined here possess much larger but fewer stomata per unit of leaf surface (i.e., stomatal density) than do modern leaves of the same Trujillo variety. Perhaps the archeological leaves reflect a real difference in the stomatal system of ancient versus recent Trujillo coca, although more samples of both archeological and modern leaves are needed to evaluate this possibility. Alternatively, the combination of large and sparse stomata may merely reflect the inverse relationship between stomatal density and the sizes of both individual leaves and their stomata, as previously noted for diverse, pantropical species of *Erythroxylum* (Rury 1981, 1982). Due to such habitat-related, morphogenetic effects upon mature coca leaf structure (for example, sun- vs. shade-form leaves), the stomatal frequency provides a more reliable basis for comparisons among coca leaves, since it integrates both stomatal size and density into a single, standard measurement.

Although the geographic origin of and ecological conditions experienced by the archeological coca leaves are uncertain, their structural conformity with the anatomical profile of modern, drought-adapted Trujillo coca from the arid Peruvian coast suggests that they were grown in a similarly xeric environment. Significantly, the coca leaf (Trujillo) illustrated by Griffiths (1930) also shows drought-adaptive anatomical details characteristic of modern Trujillo coca, such as sunken stomata sparsely distributed over the lower epidermis, and a small, lanceolate leaf morphology. This further supports the contention (Plowman, in press) that drought-resistent Trujillo coca was being grown at an early date on the desert coast of Peru.

PROBLEMS IN THE ARCHEOLOGY OF COCA

In most cases in the past, archeological coca leaves from the Peruvian coast have been identified by both botanists and archeologists as *Erythroxylum Coca* (var. *Coca*). Harms (1922) was the first botanist to identify the small-leaved coca from coastal Peruvian sites as *E. novogranatense,* since he was familiar with the taxonomic studies on *Erythroxylum* by his colleague O. E. Schulz (1907). Many authors, however, unaware of the existence of the coastal variety Trujillo coca, have suggested that the presence of archeological coca on the Peruvian coast implied extensive, early trans-Andean trade in coca from the eastern Andes to the coast (Sauer, 1950; Lanning, 1967; Cohen, 1978; Dobkin de Rios, 1981). Although trade in leaves of *E. Coca* var. *Coca* from the eastern Andes to the coast may have occurred on a small scale, there is little evidence for it from archeological remains. Only Mortimer (1901) reported and illustrated leaves of this variety from the coast (from a burial at Arica, Chile) which from the illustrations are clearly referable to *E. Coca* var. *Coca*. This suggests that at least some leaves of this variety may have been traded across the Andes but most likely Trujillo coca was the principal variety used on the coast.

Although samples of archeological coca discovered to date are limited primarily to Trujillo coca from coastal Peru, future discoveries of archeological leaves have great potential for shedding new light on the early evolution, domestication and diffusion of coca in the Andean region and may possibly serve as cultural markers for early human contacts in the area. It is hoped that this study will stimulate archeologists to search for remains in older sites and in new areas in order to elucidate further the early events in the evolution of cultivated coca.

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We are grateful to Peggy Lee Fiedler who assisted in the early stage of gathering the literature on archeological coca and to Jeff Boeke and Wade Davis for furnishing critical specimens used in this study. José Schunke V. was instrumental in providing valuable assistance during field work in Peru. Dr. María Rostworowski de Diez Canseco helped us to determine the origin of archeological specimens in Peru. Dr. Michael Mosely and Dr. Robert Feldman provided us with archeological coca specimens and alerted us to the existence of materials at the Lowie Museum of Anthropology. The Lowie Museum kindly furnished us with photographs of their specimens to illustrate the text.

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TABLE 1

ARCHEOLOGICAL COCA SPECIMENS EXAMINED (ALL REFERABLE TO *ERYTHROXYLUM NOVOGRANATENSE* VAR. *TRUXILLENSE*)

Collector	*Description*	*Provenance*	*Approximate Age*	*Museum and Accession Number*
Max Uhle[1]	Coca leaves contained in woollen bag	Peru: Dept. Arequipa. Yauca Valley, Lampilla.	Inca, Late Horizon (1476–1534 A.D.)	Lowie Museum 4-8225
Max Uhle	Coca leaves contained in woollen bag	Peru: Dept. Ica. Ocucaje. Cerro Uhle.	Late Horizon. (1476–1534 A.D.)	Lowie Museum 4-4519
Max Uhle	Coca leaves contained in woollen bag	Peru: Dept. Ica. Chulpaca.	Late intermediate period	Lowie Museum 4-4372
Max Uhle	Coca leaves contained in woven bag	Peru: Dept. Arequipa. Acarí.	"Mochica"	Lowie Museum 4-8268a
Wattis collection	Coca leaves contained in cotton bag	Peru: Dept. Ica. Taruga Valley. Atarco II site, Inca Cemetery.	Late Horizon	Lowie Museum 16-13426
John M. Blake (1836)	Coca leaves from woollen bag.	Chile: Bay of Chacota, 1.5 mi. south of Arica. Inca Cemetery.	Inca Period.	Peabody Museum, Harvard University, 13072

L. M. Stumer (1953–1955)	Fragments of coca leaves and twigs	Peru: Dept. Lima. Rimac Valley. Vista Alegre.	Probably Late Horizon	Botanical Museum, Harvard University, 10-116, 10-117.
L. M. Stumer[1] (1953–1955)	Broken coca leaves and two small endocarps	Peru: Dept. Lima. Rimac Valley. Vista Alegre.	Probably Late Horizon.	Botanical Museum, Harvard University, 10-124.
Unknown, "Nazca no. 1"[1]	Leaf fragments	Peru: Dept. Ica. Nazca region.	"Cultura Nazca"	Museo de Historia Natural 'Javier Prado'. Original material from Museo Regional de Ica.
Unknown, "Nazca no. 4"[1]	Leaf fragments from "bolsa de piel"	Peru: Dept. Ica. Nazca region.	"Cultura Nazca"	Museo de Historia Natural 'Javier Prado'. Original material from Museo Regional de Ica.
Unknown, "Nazca no. 6"[1]	Leaf fragments from "bolsa de la cultura Nazca"	Peru: Dept. Ica. Río Grande valley. Hacienda Monte Grande	"Cultura Nazca"	Museo de Historia Natural 'Javier Prado'. Original material from Museo Regional de Ica.
Unknown, "Nazca no. 8"[1]	Leaf fragments from "bolsa de la cultura Nazca"	Peru: Dept. Ica. Nazca region. Hacienda Cahuachi.	"Cultura Nazca"	Museo de Historia Natural 'Javier Prado'. Original material from Museo Regional de Ica.
J. Parsons	Four coca endocarps	Peru: Dept. Lima Chilca.	Late intermediate period (post 1100 A.D.)	J. Parsons collection.

[1] Material prepared for anatomical study.

TABLE 2

RECENT LEAF SPECIMENS OF CULTIVATED COCA (*ERYTHROXYLUM* SPP.) EXAMINED

Species & Variety	*Collector & Number* [1]	*Locality (Country & Department)* [2]	*Location of Voucher Herbarium Specimens* [3]
E. Coca Lam. var. *Coca*	Cook & Gilbert 1711*	PERU: Cuzco	US
	Plowman & Kennedy 5793	PERU: Huánuco	ECON, F, K, NCU, US, USM
	T. Plowman 5181*	BOLIVIA: La Paz	COL, ECON, P, US
	T. Plowman 5827*	PERU: Huánuco	ECON, F, K, NCU, US, USM
	T. Plowman 5830	PERU: Huánuco	ECON, F, K, NCU, USM
	T. Plowman 5833	PERU: Huánuco	ECON, F, K, NCU, USM
	T. Plowman 5839	PERU: Huánuco	ECON, F, NCU, USM
	T. Plowman 5862	PERU: Huánuco	ECON, F, NCU, USM
	T. Plowman 5932	PERU: Huánuco	F, GH, NCU, USM
	T. Plowman 5975	PERU: Huánuco	ECON, F, K, NCU, NY, SP, US, USM
	T. Plowman 6042	PERU: San Martín	AAU, ECON, F, K, NCU, US, USM
	T. Plowman 6061*	PERU: Huánuco	ECON, F, NCU, USM, VEN
	Plowman & Schunke 7510*	PERU: San Martín	ECON, F, NCU, P, USM
	Plowman *et al.* 11271	PERU: Huánuco	ECON, F, USM
	Plowman *et al.* 11272	PERU: Huánuco	ECON, F, USM
	P. M. Rury 320	PERU: Cuzco	ECON, USM
	P. M. Rury 321	PERU: Cuzco	ECON, USM
	P. M. Rury 322	PERU: Cuzco	ECON, USM
	P. M. Rury 323	PERU: Cuzco	ECON, USM
	P. M. Rury 324	PERU: Cuzco	ECON, USM

E. Coca var. *Ipadu* Plowman	E. W. Davis 10	COLOMBIA: Vaupés	ECON, GH, K, MO, NCU, P, US
	E. W. Davis 19*	COLOMBIA: Vaupés	ECON, F, K, MO, NY, US
	Plowman *et al.* 6748	PERU: Loreto	ECON, F, K, NCU, USM
	Plowman *et al.* 7136	PERU: Loreto	AAU, ECON, F, INPA, K, LA, NCU, UBC, USM, VEN
	R. Spruce 73*	BRAZIL: Amazonas	K
	J. Torres 167	PERU: Loreto	ECON, F, NCU
E. novogranatense (Morris) Hieron. var. *novogranatense*	O. F. Cook 98*	COLOMBIA: Nariño	US
	E. W. Davis 557*	COLOMBIA: Cesar	ECON, F
	Lehmann 4737*	COLOMBIA: Cauca	F, GH, K, P, US
	T. Plowman 2020*	COLOMBIA: Putumayo	COL, ECON, F, K, S, US
	Plowman & Davis 3684*	COLOMBIA: Cesar	COL, ECON, NCU
	T. Plowman 3734*	COLOMBIA: Antióquia	COL, ECON, F, S, US
	Plowman *et al.* 3768	COLOMBIA: Cauca	ECON
	T. Plowman 4144*	COLOMBIA: Huila	COL, ECON, F, US
	Plowman & Davis 4152*	COLOMBIA: Huila	COL, ECON, F, US
	Plowman & Vaughan 5272*	COLOMBIA: El Valle	COL, ECON, F, K, NCU, US, USM
	T. Plowman 5382*	COLOMBIA: Cauca	COL, ECON, F, USM
	Plowman & Vaughn 5385	COLOMBIA: Cauca	COL, ECON, F, NCU
	T. Plowman 7600 ex 5373	PERU: Lima	COL, ECON, F, K, US
	T. Plowman 7670	VENEZUELA: Caracas	COL, F, NCU, NY, U, US, VEN
	Plowman & Rury 10980	PERU: Lima	COL, ECON, F, K, MO, NY, U, US, USM

TABLE 2 *(continued)*

RECENT LEAF SPECIMENS OF CULTIVATED COCA (*ERYTHROXYLUM* SPP.) EXAMINED

Species & Variety	*Collector & Number* [1]	*Locality (Country & Department)*[2]	*Location of Voucher Herbarium Specimens*[3]
E. novogranatense var. *truxillense* (Rusby) Plowman	J. D. Boeke 854*	COLOMBIA: Nariño	F
	R. Ferreyra s.n.* (ECON 34259)	PERU: La Libertad	ECON, USM
	R. Ferreyra s.n.* (ECON 34275)	PERU: La Libertad	ECON, USM
	E. Machado 1256*	PERU: San Martín	MOL, NCSC, US
	Madison *et al.* 4447*	ECUADOR: Carchi	F, NCU, SEL
	Madison *et al.* 4920*	ECUADOR: Carchi	F, NCU, SEL
	T. Plowman 5565	PERU: Amazonas	ECON, F, NCU, RB, USM
	T. Plowman 5583*	PERU: Amazonas	ECON, F, K, NCU, US, USM
	T. Plowman 5588	PERU: Amazonas	ECON, F, NCU, USM
	T. Plowman 5600*	PERU: La Libertad	ECON, F, USM
	T. Plowman 5605	PERU: La Libertad	ECON, F, NCU, USM
	T. Plowman 5606*	PERU: La Libertad	B, ECON, F, NCU, USM, VT
	T. Plowman 5612	PERU: La Libertad	ECON, F, K, NCU, USM
	T. Plowman 5618*	PERU: La Libertad	ECON, F, USM
	T. Plowman 6228 ex 5590	USA: Cult. ex PERU: Amazonas	ECON, F, NCU

*T. Plowman 6242 ex 5583	USA: Cult. ex PERU: Amazonas	NCU
P. M. Rury 300	PERU: Cajamarca	ECON, USM
P. M. Rury 301	PERU: Cajamarca	ECON, USM
P. M. Rury 302	PERU: La Libertad	ECON, USM
P. M. Rury 303	PERU: La Libertad	ECON, USM
P. M. Rury 304	PERU: La Libertad	ECON, USM
P. M. Rury 305	PERU: La Libertad	ECON, USM
P. M. Rury 306	PERU: La Libertad	ECON, USM
H. H. Rusby s.n. (NYBG Economic Museum #5463)	Commercial sample from Parke Davis & Co., from Rusby's Materia Medica collection	ECON, F

[1]Anatomical data presented in Table 4 derived from collections marked with an asterisk (*).
[2]Localities described as country and department (state) of origin.
[3]Location of herbarium voucher specimens-herbarium designations follow Index Herbariorum ed. 7, (Holmgren, Keuken & Schofield, 1981).

TABLE 3

TAXONOMICALLY USEFUL LEAF STRUCTURAL FEATURES OF THE CULTIVATED COCAS (*ERYTHROXYLUM* SPP. & VARS.)

CHARACTER	UTILITY
Prominence of central panel*	Typologically useful; most variable among leaves of Trujillo coca.
Leaf venation patterns	Typologically useful (see Table 4)
Adaxial crest above midvein*	Limited value typologically.
Presence and nature of midvein fibrous sheathing (pericycle)	Typologically useful; most variable in Trujillo coca.
Veinlet termination numbers*	Ecologically and biometrically variable within each variety.
Guard cell length*	Ecologically and biometrically variable within each variety
Stomatal density and frequency*	Ecologically and biometrically variable within each variety
Leaf thickness*	Ecologically and biometrically variable within each variety

*Indicates characters which are most reliable when used with other morphological, ecological and geographic data.

TABLE 4

LEAF VENATION PATTERNS OF THE CULTIVATED COCAS (*ERYTHROXYLUM* SPP.)

	E. Coca Lam. (including var. *Coca* & var. *Ipadu* Plowman	*E. novogranatense* var. *truxillense* (Rusby) Plowman	*E. novogranatense* var. *novogranotense*
BASIC PATTERN	Intergrading series of patterns occur both within and between these varieties: festooned eucamptodromous *to* transitional (intermediate) *to* festooned brochidodromous.		
SECONDARY VEINS	Many (15–40), closely spaced and moderately thick veins; diverging from the midvein at wide acute or 90 degree angles; following a regular, initially straight and exmedially upcurving course.	Generally similar to those of *E. Coca*, but exhibiting the full range of variation between typical leaves of *E. Coca* and *E. novogranatense* var. *novogranatense*.	Fewer (8–18), more widely spaced, slender veins than *E. Coca;* diverging at narrow to wide acute angles; following a less regular, exmedially upcurving course than in typical leaves of *E. Coca*.
INTERCOSTAL AREAS	Relatively numerous and regular in size and shape.	Relatively numerous and regular in size and shape as in *E. Coca* or intermediate between typical leaves of *E. Coca* and *E. novogranatense* var. *novogranatense*.	Fewer, larger and less regular in shape than in typical specimens of *E. Coca* and *E. novogranatense* var. *truxillense*.

TABLE 4 *(continued)*

LEAF VENATION PATTERNS OF THE CULTIVATED COCAS
(*ERYTHROXYLUM* SPP.)

INTERSECONDARY VEINS	Composite in origin from tertiary veins; similar to secondary veins in divergence and course.	Generally very similar to *E. Coca* or intermediate between those of *E. Coca* and *E. novogranatense* var. *novogranatense*.	Similar to, but usually more numerous per intercostal area than, those of *E. Coca*.
TERTIARY VENATION	Diverge from secondary veins at variable angles and form many small, non-oriented areoles of irregular size and shape.	Form many non-oriented areoles that are of a size intermediate between those of *E. Coca* and *E. novogranatense* var. *novogranatense*.	Similar to, but usually fewer and larger tertiary areoles than, those in *E. Coca* and *E. novogranatense* var. *truxillense*.
HIGH ORDER VENATION	Well developed, random or nearly orthogonal network of veinlets.	Most similar to *E. Coca*, but with full range of expression between the two species.	Generally an incomplete, random network with more veinlet termini than *E. Coca*.

TABLE 5

SELECTED ANATOMICAL FEATURES OF ARCHEOLOGICAL AND MODERN COCA LEAVES (*ERYTHROXYLUM* SPP.)

Species and Variety	*Epidermal Papillae*	*Leaf Thickness*	*Veinlet Termini*	*Stomatal Density*	*Stomatal Length*	*Stomatal Frequency*
E. Coca var. *Coca*	+	270 μm (166–576)	20.5 mm^{-2} (16–25)	389 mm^{-2} (341–448)	20.7 μm (20–22)	16.3% (15–18)
E. Coca var. *Ipadu*	+	281 μm (138–424)	20 mm^{-2} (-20-)	444 mm^{-2} (-444-)	20 μm (-20-)	16% (-18-)
E. novogranatense var. *novogranatense*	+	358 μm (212–505)	22 mm^{-2} (-22-)	247 mm^{-2} (-247-)	20 μm (-20-)	8% (-8-)
E. novogranatense var. *truxillense*						
Recent	+	295 μm (193–455)	36 mm^{-2} (25–52)	404 mm^{-2} (379–455)	21 μm (18–25)	18% (13–25)
Archeological	+/−	–	22 mm^{-2} (16–30)	183 mm^{-2} (156–203)	25 μm (-25-)	11.4% (10–13)

NOTE: Overall means given; range of specimen means shown in parentheses.
Data are derived from specimens marked with an asterisk (*) in Tables 1 and 2

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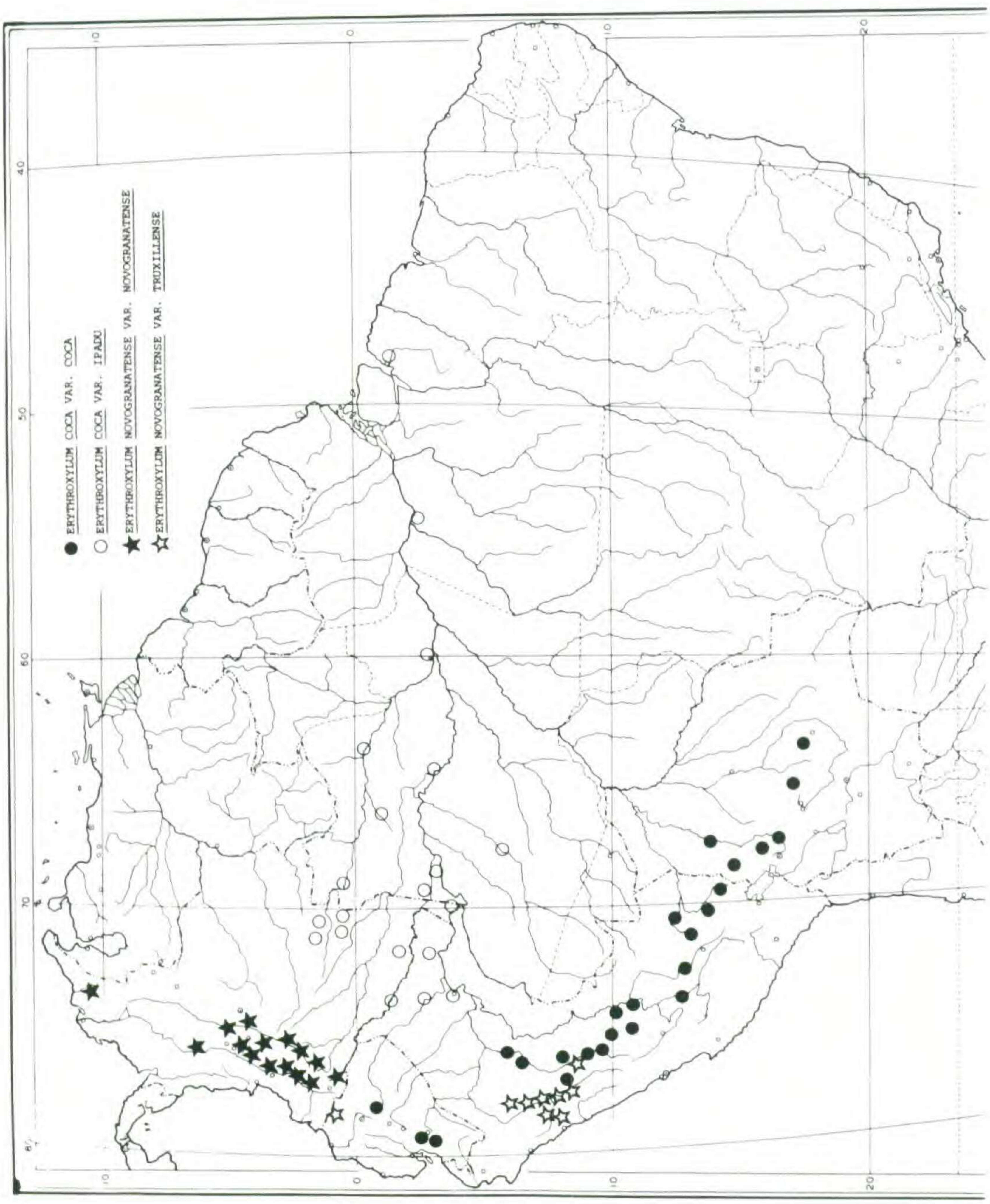
PLATE 32



ERYTHROXYLUM COCA VAR. COCA
ERYTHROXYLUM COCA VAR. IPADU
ERYTHROXYLUM NOVOGRANATENSE VAR. NOVOGRANATENSE
ERYTHROXYLUM NOVOGRANATENSE VAR. TRUXILLENSE

Plate 32. Present distribution of the four varieties of cultivated coca based on herbarium collections: closed circles, *E. Coca* var. *Coca;* open circles, *E. Coca* var. *Ipadu;* closed stars, *E. novogranatense* var. *novogranatense;* open stars, *E. novogranatense* var. *truxillense.*

PLATE 33

Plate 33. Cotton bag containing leaves of Trujillo coca (*E. novogranatense* var. *truxillense).* From an Inca cemetery, Atarco II Site, Taruga Valley, Nazca, Peru. Wattis Collection. Lowie Museum of Anthropology accession no. 16-13426. Photograph courtesy of the Lowie Museum of Anthropology. Centimeter scale.

PLATE 34

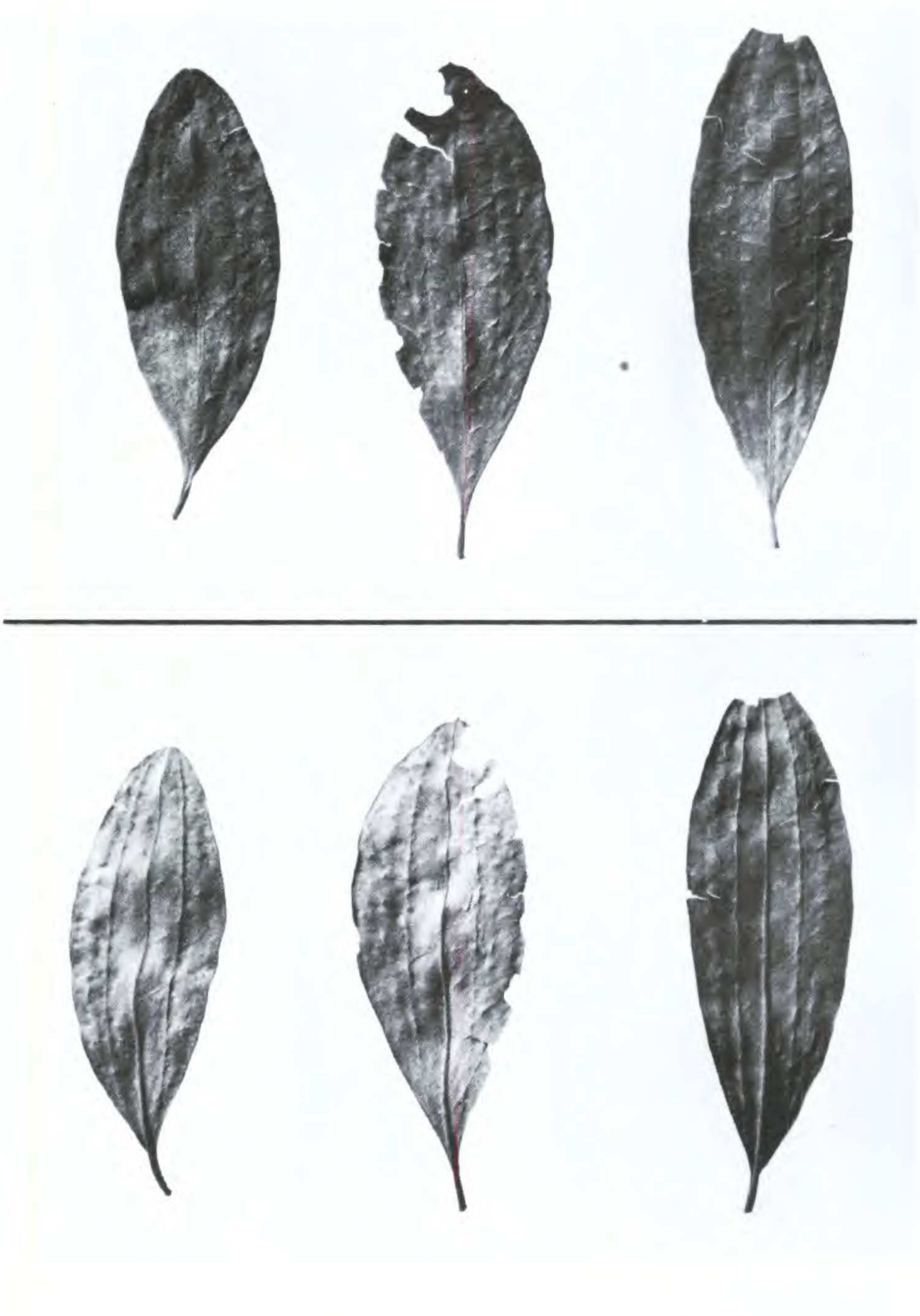


Plate 34. Leaves of Trujillo coca (*E. novogranatense* var. *truxillense*) from a cotton bag found in an Inca cemetery, Atarco II Site, Taruga Valley, Nazca, Peru. Wattis Collection. Lowie Museum of Anthropology accession no. 16-13426. Upper panel showing adaxial surface of leaves; lower panel showing abaxial surface. Photograph courtesy of the Lowie Museum of Anthropology. Millimeter scale.

PLATE 35

Plate 35. Red tapestry woollen pouch containing leaves of Trujillo coca (*E. novogranatense* var. *truxillense*). Late Horizon (Inca). Collected by Max Uhle. Lampilla, Yauca Valley, Dept. Arequipa, Peru. Lowie Museum of Anthropology accession no. 4-8225. Photograph courtesy of Lowie Museum of Anthropology. Centimeter scale.

PLATE 36

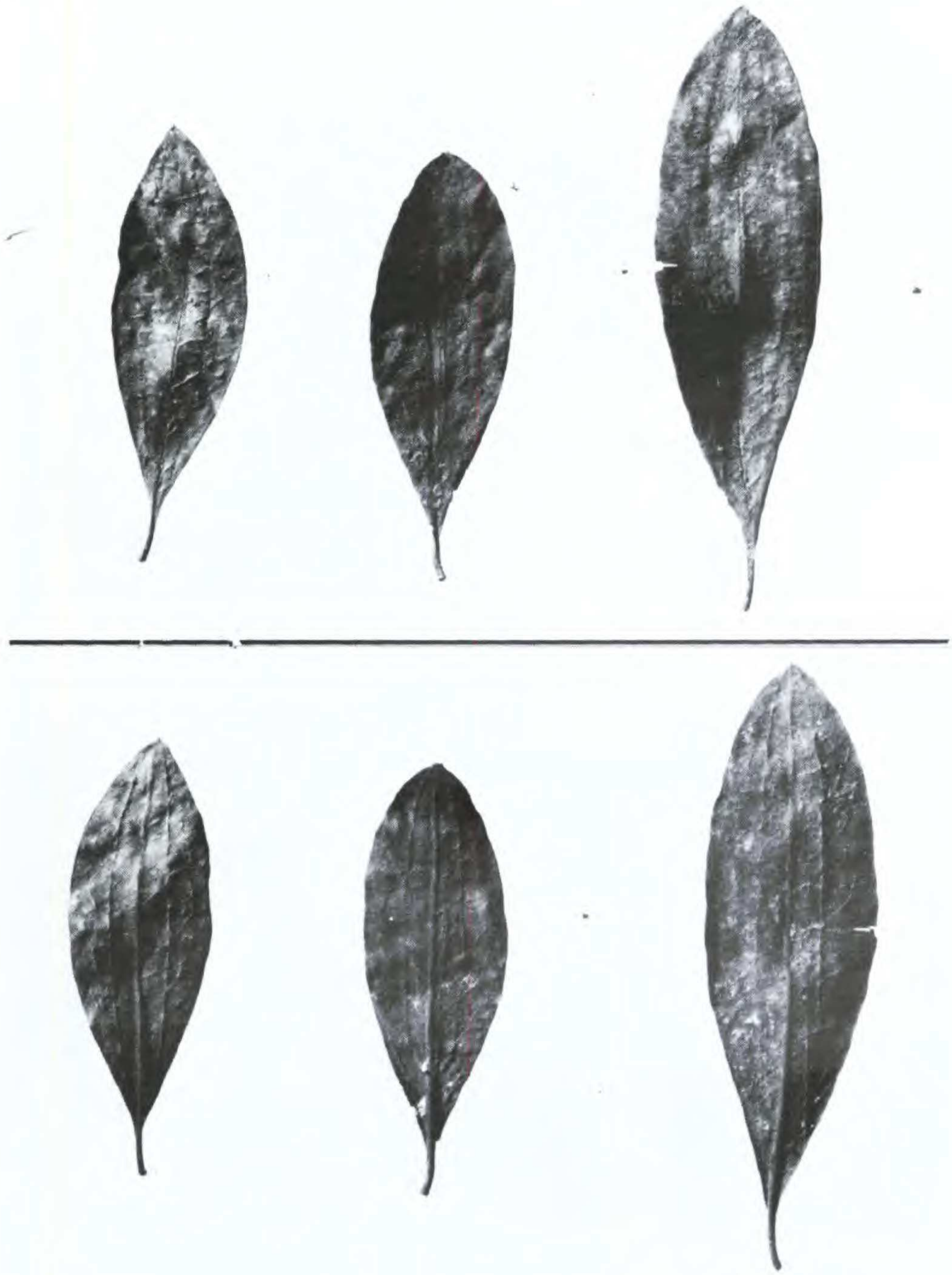


Plate 36. Leaves of Trujillo coca (*E. novogranatense* var. *truxillense*) from a woollen pouch. Late Horizon (Inca). Collected by Max Uhle. Lampilla, Yauca Valley, Dept. Arequipa, Peru. Lowie Museum of Anthropology accession no. 4-8225. Upper panel showing adaxial surface of leaves; lower panel showing abaxial surface. Photograph courtesy of the Lowie Museum of Anthropology. Millimeter scale.

Plate 37. Archeological and recent leaves of Trujillo coca (*E. novogranatense* var. *truxillense*). **A.** Camera lucida drawing of cleared leaf of Lowie Museum of Anthropology accession no. 4-8225 (see Plate 35). Centimeter scale. **B.** Camera lucida drawing of cleared leaf of *Plowman 6228 ex 5590.* Centimeter scale. **C.** Camera lucida drawing of cleared leaf of Harvard Botanical Museum Ethnobotanical accession no. 10–124. Centimeter scale. **D.** Camera lucida drawing of upper epidermis of cleared leaf, specimen "Nazca no. 4". Scale = 50 μm (micrometers). **E.** Camera lucida drawing of lower epidermis of cleared leaf, specimen "Nazca no. 8" Scale = 50 μm (micrometers). **F.** Camera lucida drawing of lower epidermis of cleared leaf showing papillae and stomata, specimen "Nazca no. 1". Scale = 50 μm (micrometers). **G.** Camera lucida drawing of lower epidermis, showing papillae and stomata, *Plowman 6228 ex 5590.* Scale = 50 μm (micrometers).

PLATE 37

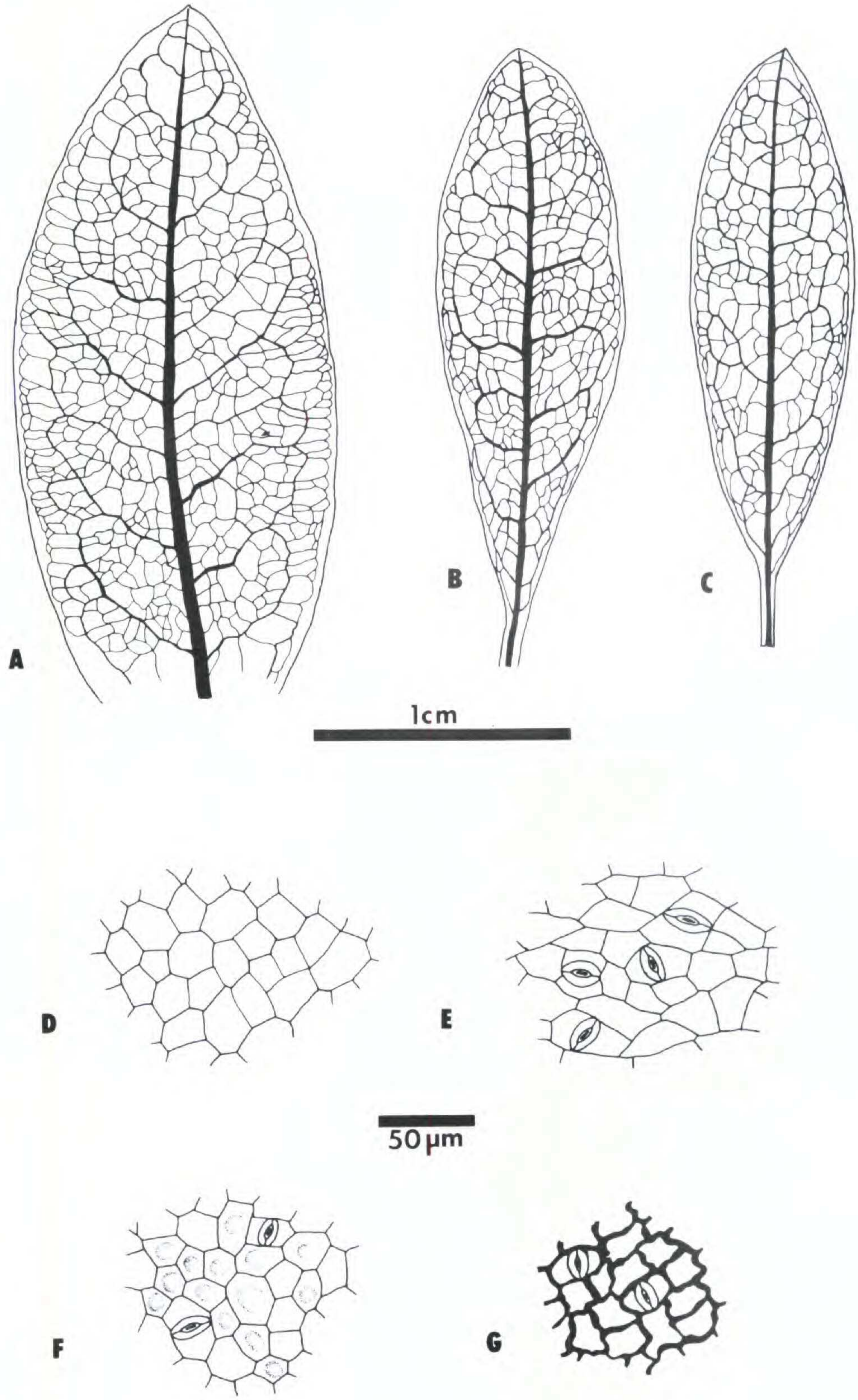


Plate 38. Archeological leaf specimens of Trujillo coca (*E. novogranatense* var. *truxillense*). Photomicrographs of cleared leaves, taken with partially polarized light. Crystals and lignified tissues (veins) appear bright white due to their positive birefringence in polarized light. Scale markers all = 100 μm (micrometers). **A.** Midvein, secondary and high order venation; note numerous crystals which appear as white flecks along veins and in mesophyll. Specimen "Nazca no. 8". **B.** Midvein with secondary vein, tertiary vein and high order venation; note numerous crystals as in Plate 38A, but mostly in mesophyll. Cleared leaf specimen, Harvard Botanical Museum accession no. 10–124. **C.** Midvein and diverging secondary vein with many crystals. Cleared leaf specimen "Nazca no. 4". **D.** Close-up of veinlet of "Nazca no. 4, shown at lower magnification in Plate 38C, revealing crystals along veinlet.

PLATE 38

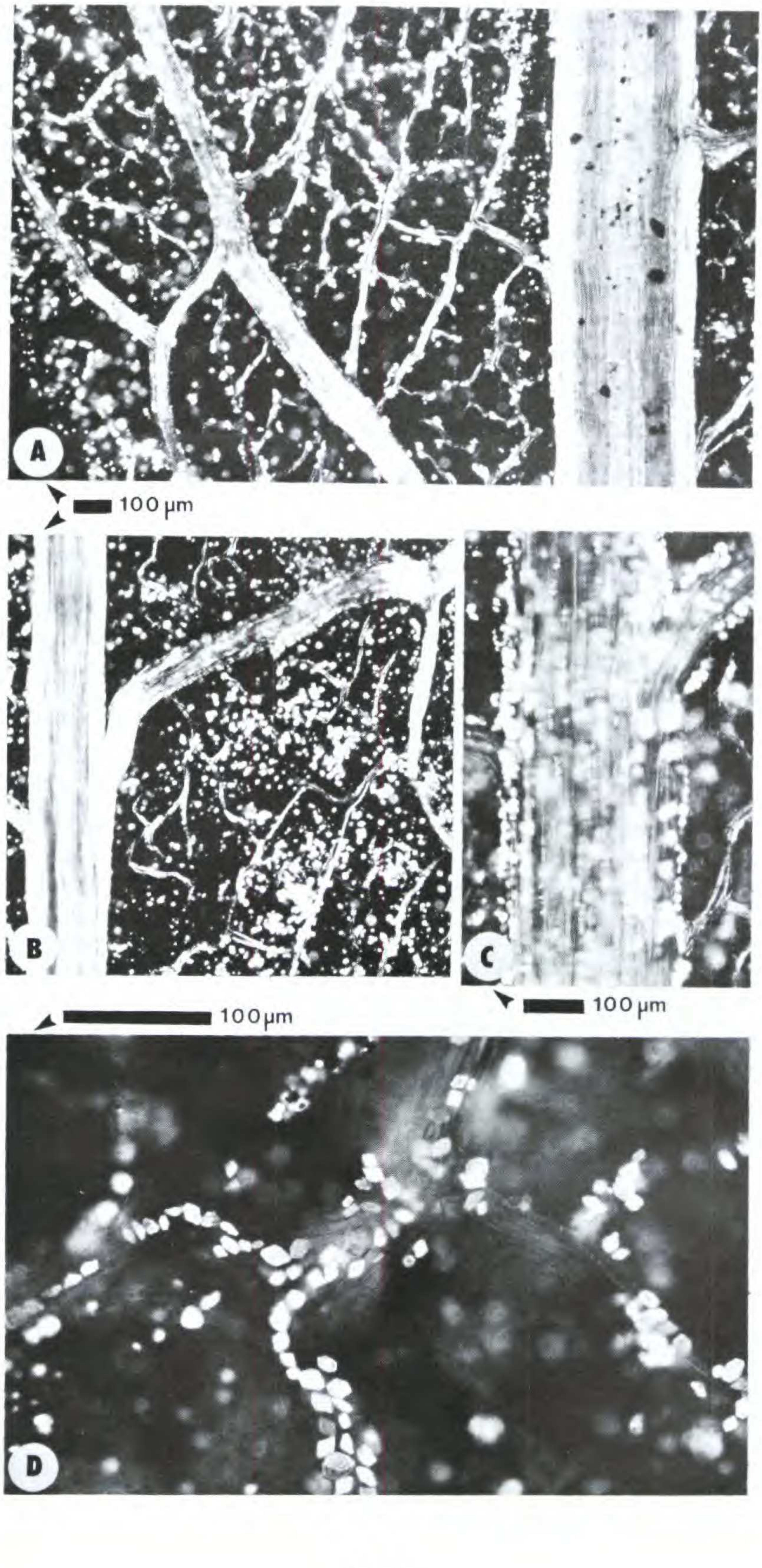


Plate 39. Leaf venation and geographic distribution of the cultivated cocas (*Erythroxylum* spp.). Centimeter scale. This map is the same as that presented in Plate 32. **A.** *E. novogranatense* var. *truxillense* (Trujillo coca), *Madison et al. 4447.* **B.** *E. novogranatense* var. *truxillense* (Trujillo coca), *Madison et al. 4920.* **C.** *E. novogranatense* var. *novogranatense* (Colombian coca), *Plowman 3734.* **D.** *E. novogranatense* var. *truxillense* (Trujillo coca), *Plowman 6242 ex 5583,* glasshouse cultivated progeny (seed) of specimen illustrated in Plate 39E. Note much larger, shade-leaf form of this glasshouse plant as compared with its parent in 39E. **E.** *E. novogranatense* var. *truxillense* (Trujillo coca), *Plowman 5583.* Typical sun-form leaf of parent of glasshouse plant shown above in Plate 39D. **F.** *E. novogranatense* var. *novogranatense* (Colombian coca), *Plowman and Davis 4152.* **G.** *E. novogranatense* var. *truxillense* (Trujillo coca), *Plowman 5600.* **H.** *E. novogranatense* var. *truxillense* (Trujillo coca), *Plowman 5618.* Note the size differences between this and *Plowman 5600* (Plate 39G), from the same locality. **I.** *E. novogranatense* var. *novogranatense* (Colombian coca), *Plowman 7600 ex 5373,* planted from seed by Plowman in Lima in 1976. **J.** *E. Coca* var. *Coca* (Bolivian coca), *Plowman 5827,* local name "molle coca". **K.** *E. Coca* var. *Coca* (Bolivian coca), *Plowman 7510.* **L.** *E. Coca* var. *Ipadu* (Amazonian coca), *Spruce 73.*

PLATE 39

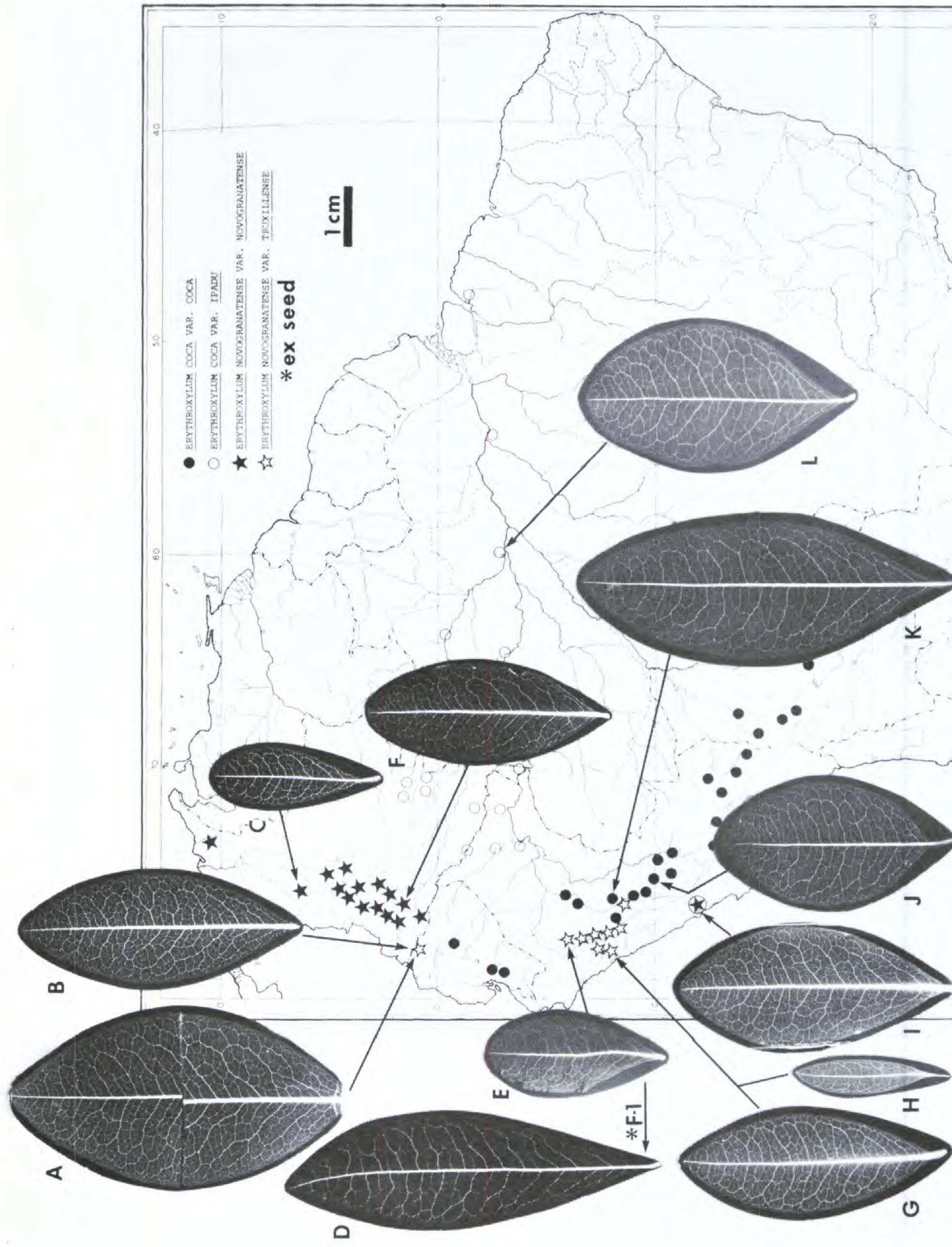

ERYTHROXYLUM COCA VAR. COCA
ERYTHROXYLUM COCA VAR. IPADU
ERYTHROXYLUM NOVOGRANATENSE VAR. NOVOGRANATENSE
ERYTHROXYLUM NOVOGRANATENSE VAR. TRUXILLENSE
*ex seed
1cm
A
B
C
D
E
*F-1
F
G
H
I
J
K
L

Plate 40. High order venation of recent, cleared leaves of the cultivated cocas (*Erythroyxlum* spp.). Photomicrographs taken without polarized light. Scale markers = 100 μm (micrometers). **A.** *E. novogranatense* var. *novogranatense* (Colombian coca), *Plowman and Davis 3684.* **B.** *E. novogranatense* var. *truxillense* (Trujillo coca), *Boeke 854.* **C.** *E. novogranatense* var. *truxillense* (Trujillo coca), *Plowman 5606.*

PLATE 40